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REVIEW

Florian P. Schiestl

On the success of a swindle: pollination by deception in orchids

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Abstract A standing enigma in pollination ecology is the evolution of pollinator attraction without offering reward in about one third of all orchid species. Here I review concepts of pollination by deception, and in particular recent findings in the pollination syndromes of food deception and sexual deception in orchids. Deceptive orchids mimic floral signals of rewarding plants (food deception) or mating signals of receptive females (sexual deception) to attract pollen vectors. In some food deceptive orchids, similarities in the spectral reflectance visible to the pollinator in a model plant and its mimic, and increased reproductive success of the mimic in the presence of the model have been demonstrated. Other species do not mimic specific model plants but attract pollinators with general attractive floral signals. In sexually deceptive orchids, floral odor is the key trait for pollinator attraction, and behaviorally active compounds in the orchids are identical to the sex pheromone of the pollinator species. Deceptive orchids often show high variability in floral signals, which may be maintained by negative frequency-dependent selection, since pollinators can learn and subsequently avoid common deceptive morphs more quickly than rare ones. The evolution of obligate deception in orchids seems paradoxical in the light of the typically lower fruit set than in rewarding species. Pollination by deception, however, can reduce self-pollination and encourage pollen flow over longer distances, thus promoting outbreeding. Although some food deceptive orchids are isolated through postzygotic reproductive barriers, sexually deceptive orchids lack post-mating barriers and species isolation is achieved via specific pollinator attraction. Recent population genetic and phylogenetic investigations suggest gene-flow within subgeneric clades, but pollinator-mediated selection may maintain species-specific floral traits.

F. P. Schiestl (✉)
Geobotanical Institute, ETH Zürich,
Zollikerstrasse 107,
CH-8008 Zürich
e-mail: florian.schiestl@env.ethz.ch
Tel.: +41-1-6327429
Fax: +41-1-6321463

Introduction

The discovery of pollination by deception dates back to Christian Konrad Sprengel, who reported in his book on the "discovery of the secret of nature in the structure and fertilization of flowers" the absence of nectar in several species of orchids that he called "Scheinsaftblumen," sham nectar flowers, and proposed a system of deception for the maintenance of pollinator visits (Sprengel 1793). This interpretation was met with disbelief by such distinguished naturalists as Charles Darwin, who, although confirming the absence of nectar in many orchids, wrote in his seminal book on orchid pollination that it seemed "utterly incredible" to him that "bees (. . .) should persevere in visiting flower after flower of the above named Orchids, (. . .) in the hope of obtaining nectar which is never present" (Darwin 1885). In the early 1900s, Pouyanne (1917) and Coleman (1927) discovered independently that some orchids, without producing nectar, mimic mating signals of insects and are pollinated by males attempting copulation on the flowers. It took some more years to establish the fact that many orchids never produce a floral reward but imitate attractive signals to swindle their pollinators (Daumann 1971; Faegri and van der Pijl 1979). This imitation can involve signals that are of importance for the pollinator in various biological contexts such as brood substrate-or food searching, and mating (Wiens 1978; Vogel 1993). So-called food deceptive species imitate a range of floral attractants, such as floral shape, color, and scent, that are associated by the pollinators with an edible reward (Fig. 1; Vogel 1983; Nilsson 1983, 1992; Dafni 1984; Dafni 1987; Roy and Widmer 1999). Although food deception is widespread among plants (Vogel 1993; Thakar et al. 2003), it is especially frequent in orchids with about one third of the family, approximately 10,000 species being food deceptive (Dafni 1984; Ackerman 1986; Nilsson 1992). Furthermore, this pollination strategy has evolved repeatedly in independent orchid lineages (Johnson et al. 1998; Cameron et al. 1999; Cozzolino et al. 2001; Bateman et al. 2003). Arguably the most spectacular case of floral mimicry is sexual deception, up to now exclusively known in orchids, where flowers

Fig. 1 Contrasting the two deceptive pollination systems food deception and sexual deception. **a** *Anacamptis morio* with one of its pollinators, *Bombus pascuorum* in southern Italy (courtesy C. Salzmann). **b** A flower of the sexually deceptive *Ophrys sphegodes* with its pollinator, a male of the solitary bee *Andrena nigroaenea*. The male carries pollinaria of this orchid on its head

imitate mating signals of certain insect species and are pollinated by sexually aroused males, that mistake the flower for a female and pollinate it during a "pseudocopulation" (Fig. 1). Like food deception, sexual deception has also evolved multiple times being represented by the European genus *Ophrys,* South African *Disa* and nine Australian genera, altogether comprising about 400 described species (Dafni and Bernhardt 1990; Steiner et al. 1994; Pridgeon et al. 1997). However, this pollination syndrome is probably more widespread as currently known, because new cases have been described recently in some genera of neotropical Maxillariinae, and Pleurothallidinae (Singer 2002; Singer et al. 2004; Blanco and Barboza 2005). Among the latter group, sexual deception may be prevalent in the large genus *Lepanthes* (>800 species; Blanco and Barboza 2005). Additionally, anecdotic evidence exists for other orchid genera (van der Pijl and Dodson 1966; Yadav 1995) and even one case outside the orchid family has been proposed (Rudall et al. 2002). Sexual deception differs from food deception by the exclusive attraction of male insect pollinators that have the motivation of mating rather than searching for food. Accordingly, pollination is often species-specific and floral odor, a mimicry of the pollinators sex pheromone, is crucial for pollinator attraction (Paulus and Gack 1990; Borg-Karlson 1990; Bower 1996; Schiestl et al. 1999).

Although pollination by deception has attracted great interest from ecologists and evolutionary biologists, its spectacularly diverse evolution among orchids still poses many unsolved questions. Here I review concepts of pollination by deception and recent, significant advances in our understanding of proximate and ultimate causes in this fascinating topic of ecology and evolution. I will limit this review to the pollination syndromes of food deception and sexual deception in orchids, because most research has focused on these two systems.

Floral mimicry: how to cheat a pollinator

Zoophilic plants attract pollen vectors with floral signals that are associated with rewards or release innate responses in the pollinators (Faegri and van der Pijl 1979; Vogel 1983). Deceptive plants face the challenge of repeatedly attracting pollinators that often rapidly learn and avoid non-rewarding plants (Ackerman 1986; Ayasse et al. 2000). To do so, these plants imitate signals attractive to pollinators, a phenomenon called floral mimicry. Two types of mimicry are generally recognized among deceptive flowers. The first is Batesian mimicry in a strict sense, consisting of a "mimic" that imitates signals of a "model", and an "operator" that responds to them (Fig. 2; Wickler 1968; Wiens 1978; Dafni and Ivri 1981; Dafni 1984; Dafni 1987). Alternatively, a model species may not exist, but plants mimic general floral signals such as bright colors and floral scent, a phenomenon termed generalized-, or non-model mimicry (Nilsson 1983; Nilsson 1992). This discrimination between two types of mimicry is important as it predicts different evolutionary outcomes (Dafni 1983; Nilsson 1992). In Batesian mimicry, the reproductive success of a mimic depends on its frequency relative to the model and the capabilities of the operator to discriminate between

Fig. 2 Comparison of model and mimic in an Australian sexually deceptive pollination system. Two females of *Neozeleboria cryptoides* are shown with a labellum of a *Chiloglottis trapeziformis* flower. The size of the flower and its 100 times larger production of the attractive odor compound suggest that it represents a supernormal stimulus for males (Schiestl 2004)

model and mimic. Hence, mimics will be selected to be less common than models and minimize discrimination and avoidance learning by operators, resulting either in stabilizing selection for similarity to the model (Nilsson 1983), or maintenance of exaggerated floral signals at an optimal level for pollinator responses (Schiestl 2004). In generalized mimicry, plants often bloom gregariously and may, rather than resembling any of the co-blooming species, produce large, showy floral displays. In this system, polymorphisms in floral traits are thought to delay avoidance learning by the operator (Heinrich 1975; Ackerman 1981; Dafni 1984; Nilsson 1992; Petterson and Nilsson 1993). Pollination success in these plants does not depend on their frequency relative to any specific model species, but on the abundance of a rewarding plant community. Two contrasting predictions have been proposed for this relationship and both are supported by empirical evidence: the *remote habitat hypothesis* predicts that mimics will do best in habitats with few rewarding plants because rewarding and deceptive plants compete for pollinators (Lammi and Kuitunen 1995). Such an effect was found in *Dactylorhiza sambucina* in Finland. In contrast, the *magnet species effect* predicts that mimics profit from an abundance of rewarding plants that attract potential pollinators (Thompson 1978; Laverty 1992), which has been demonstrated in the food deceptive orchid *Anacamptis morio* in Sweden (Johnson et al. 2003b).

Although generalized mimicry is assumed to be common among food deceptive plants (Dafni 1984), Batesian mimicry has been demonstrated only rarely among food deceptive species, but is well established in sexually deceptive orchids. Evidence for Batesian mimicry requires a number of assumptions to be met. Obviously model and mimic must be sympatric and co-blooming, and the mimic must occur at lower frequency than the model, since operators may eventually learn and avoid the mimic. The mimicry must be advantageous for the mimic, i.e. the reproductive success of the mimic must be higher when the model is present (Wiens 1978; Nilsson 1983; Dafni 1984; Ackerman 1986; Johnson 1994; Roy and Widmer 1999). This assumption is, however, difficult to discriminate from the "magnet species effect," and thus studies should control for co-blooming, rewarding non-model plants. A crucial part of a Batesian mimicry is that the operator (pollinator) initially does not discriminate between the model and mimic (Wiens 1978), and hence the floral signals of model and mimic must be similar *for the pollinators senses*. Modern analytical and physiological tools have enabled the testing of this latter assumption, which has led to amazing insights into the mechanisms of floral mimicry.

Pollinators and floral signals

Food deception

Food deceptive orchids are pollinated by a large array of different insects. Bees are the most important pollinators of many species, but butterflies, moths, flies, and beetles are also exploited by some orchids (e.g. Nilsson 1979; Nilsson 1980; Nilsson 1983; Nilsson 1984; Petterson and Nilsson 1993; Johnson and Steiner 1997; Steiner 1998; Roubik 2000; Johnson 2000). Visual signals are thought to be of primary importance for pollinator attraction in food deceptive systems. Behavioral experiments and field observations have shown that bees prefer, after being rewarded, flowers of similar color, thus indicating selection for corolla color similarity in mimics and potential model species (Gumbert and Kunze 2001; Gigord et al. 2002; Johnson et al. 2003a). Such selection may, however, be mitigated by the temporal and spatial dynamics of co-blooming plant communities, explaining the lack of a specific model species in generalized mimicry systems. A few examples of Batesian mimicry, however, are well documented, such as *Cephalanthera rubra*, *Disa ferruginea*, and *D. pulchra* and their respective models, where similarities between model and mimic in color reflectance spectra visible to the pollinator have been reported (Nilsson 1983; Johnson 1994; Johnson 2000). In a more elaborate approach, Galizia et al. (2005) mapped visual signals on the perceptual space of honey bees and confirmed similarities in *Anacamptis israelitica* and its suspected model *Bellevallia flexuosa*.

Many species of food deceptive orchids emit floral odor (Nilsson 1979; Nilsson 1983; Nilsson 1984; Bergström et al. 1992; Moya and Ackerman 1993; Ackerman et al. 1997; Barkman et al. 1997; Salzmann and Schiestl unpublished), but little is known about similarities of mimics and potential model species. In comparing floral odor of *Anacamptis israelitica* and *B. flexuosa* and its perception in the honeybee brain, Galizia et al. (2005) found no evident similarity in this floral trait. In behavioral experiments with bumble bees foraging on artificially scented flower dummies, Kunze and Gumbert (2001) showed that discrimination of model and mimic by bumble bees is greater if scents can be used to identify the mimic, however, discrimination is poorest if the floral odor of model and mimic is identical. Therefore, mimics should be selected to produce floral odor identical to their models or avoid odor production altogether. These experiments provide intriguing hypotheses that should be tested in future studies to better understand how odor influences floral mimicry.

Sexual deception

The major pollinators of sexually deceptive orchids are aculeate Hymenoptera, but other Hymenoptera as well as Diptera are also involved (Dafni and Bernhardt 1990; Borg-Karlson 1990; Peakall 1990; Paulus and Gack 1990; Steiner et al. 1994; Bower 1996; Schiestl et al. 2004; Blanco and Barboza 2005). In sexually deceptive orchids, Batesian mimicry is easily conceivable with the females of the pollinator species being the model, and males the operator in the system. Earlier studies demonstrated similarities in shape, color, and pilosity of model and mimic (Kullenberg 1961; Ågren et al. 1984), and more recent investigations have focused on odor signals that are of primary importance for the attraction of the operators (Fig. 3; Borg-Karlson 1990; Schiestl et al. 1997; Schiestl et al. 1999; Ayasse et al. 2003;

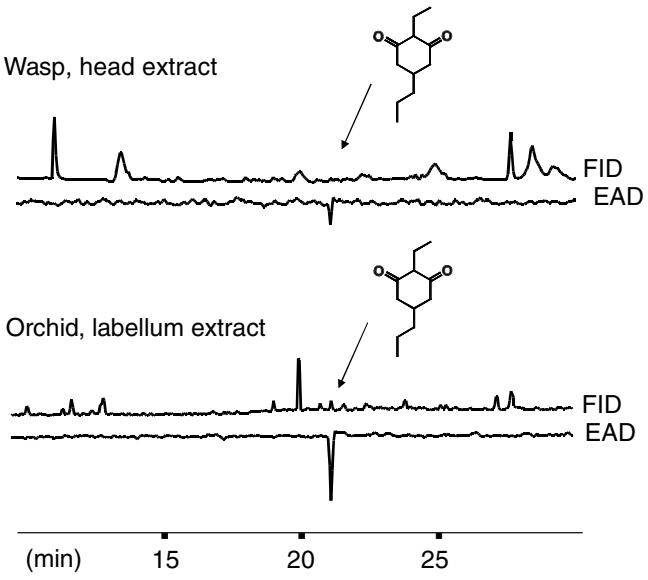

Fig. 3 Gas chromatographic analyses with electroantennographic detection (GC-EAD) of the sex pheromone of *Neozeleboria cryptoides* (female of the pollinator wasp, model) and *Chiloglottis trapeziformis* labellum extract (mimic). In this analysis, flame ionization detection (FID) and electroantennographic detection (EAD) were recorded simultaneously using an antenna of a male wasps. One compound, termed "Chiloglottone," was active in olfactory neurons of male wasps and showed strong attractiveness to males in field tests (Schiestl et al. 2003)

Schiestl et al. 2003; Schiestl et al. 2004). A major breakthrough in the identification of active compounds has recently been achieved by applying electrophysiological tools in combination with analytical chemistry. This approach allows the separation of odor blends and a simultaneous survey of individual compounds for biological activity in olfactory neurons (Fig. 3; Schiestl and Marion-Poll 2002). Using this technique, it was shown that only a subset of the emitted floral odor compounds trigger behavioral responses in the pollinators. These "biologically active compounds" are identical to the sex pheromones produced by the females of the pollinator insects (Schiestl et al. 1999; Ayasse et al. 2003; Schiestl et al. 2003). In the European *Ophrys sphegodes*, active compounds are simple, more or less ubiquitous constituents of plant cuticular hydrocarbons, that release behavioral activity only in specific relative amounts (Schiestl et al. 2000, Schiestl and Ayasse 2002). A primary function of these compounds, that are a part of the wax layer on the cuticle, is to prevent dehydration, and pollinator attraction seems to have evolved secondarily through a shift in function (Schiestl et al. 1999). In another *Ophrys* species, however, less common compounds, namely oxo- and hydroxy acids attract the pollinators, males of a scoliid wasp (Ayasse et al. 2003), suggesting high flexibility in the evolution of pollinator attracting signals within *Ophrys*. Even more peculiarly, the Australian *Chiloglottis trapeziformis*, attracts its pollinator with a single compound, termed Chiloglottone, that represents an as yet unknown class of natural products (Schiestl et al. 2003). This apparent diversity in mechanisms of chemical communication, even among the few species investigated in detail, suggests that the dominant role of certain hymenopteran groups as pollinators of sexually deceptive orchids cannot be explained by constraints in chemical communication, but ecological factors such as specific behavioral traits of these pollinators may explain their preferred exploitation by these orchids.

Pollinator behavior and selection on plants

Pollinator behavior influences reproductive success and gene flow within and among plant populations and may thus impose selection on plants that are pollinator-limited in their reproductive success, a condition frequently found among deceptive orchids (Tremblay et al. 2005). Pollinator-imposed selection on floral traits is generally stronger when pollination is specific, as selection will be influenced by the more uniform behavioral patterns of one or few pollinator species. Specificity in pollination is common among deceptive orchids (Nilsson 1992; Tremblay 1992), and especially pronounced among sexually deceptive species (Paulus and Gack 1990; Bower 1996). An important aspect of pollinator behavior is the usually high capacity of flower visitors to associate deception with certain floral signals and thus avoid non-rewarding flowers. This is prevalent even in sexually deceptive flowers, were floral signals release innate behavioral patterns (Ayasse et al. 2000). Besides pollinator behavior, pollinator morphology also imposes selection on flowers and has, for example, been shown to drive the evolution of spur length (Nilsson 1988; Johnson and Steiner 1997), but here I will focus on behavioral patterns of pollinators.

Pollinator learning and negative frequency-dependent selection

Deceptive orchids often show a remarkable degree of variation in floral traits such as color (Nilsson 1980; Petterson and Nilsson 1993; Johnson 1994; Gigord et al. 2001) and scent (Ackerman 1986; Ackerman et al. 1997; Moya and Ackerman 1993; Schiestl et al. 1997; Barkman et al. 1997; Ayasse et al. 2000; Salzmann and Schiestl unpublished). A possible explanation for the maintenance of these polymorphisms is negative frequency-dependent selection. This type of selection is a likely outcome of the learning and avoidance of individual flowers or flower morphs by the pollinators, since common morphs will be avoided more quickly than rare ones and hence face fitness disadvantages (Heinrich 1975; Ackerman et al. 1997; Smithson and Macnair 1996; Gigord et al. 2001). In many floral mimicry systems, pollinators are able to learn and subsequently avoid the mimic, although they might initially not discriminate between model and mimic (Dafni 1984; Peakall 1990; Paulus and Gack 1990; Ayasse et al. 2000). An example of switching between different color morphs after an unrewarding visit are bumble bees that pollinate *Dactylorhiza sambucina*, a food deceptive orchid occurring in purple and yellow flower morphs (Gigord et al.

2001). This behavior leads to overvisitation of the rarer morph and may explain the maintenance of the two forms in stable frequency within a population. In a survey of natural populations in the same species, Pellegrino et al. (2005) found, however, no evidence for negative frequency-dependent selection, but a positive correlation between the frequency of yellow morphs and the reproductive success of both morphs. In an experimental approach with painted flowers, Aragon and Ackerman (2004) also did not detect negative frequency-dependent selection on flower color in the polymorphic *Psychilis monensis*. Besides flower color, pollinator-imposed selection may act on floral odor, a trait that is generally learned faster in bee-pollinators than color (Bogdany 1978; Menzel 1985). In *Tolumnia variegata,* however, negative frequency-dependent selection seems not to explain odor polymorphism, but in this case odor variation was only assessed as overall presence/absence of scent and not at the individual-compound level (Ackerman et al. 1997). Individual compounds in the floral odor of the deceptive *Anacamptis morio* vary significantly more compared to the rewarding *A. coriophora*, possibly as an outcome of negative frequency-dependent selection in the deceptive species versus stabilizing selection in the food rewarding species (Salzmann and Schiestl unpublished).

Potential for negative frequency-dependent selection on floral odor has also been shown in the sexually deceptive *Ophrys sphegodes*, where pollinators learn and subsequently avoid the odor bouquet of individual flowers (Ayasse et al. 2000). Although pollinator behavior often predicts negative frequency-dependent selection, its potential impact on complex traits such as scent is difficult to assess, because the behavioral significance of individual compounds is often unknown.

Pollinator preferences and selection

Among the floral traits potentially influenced by pollinator's preferences, flower height and size have received most attention. Some studies on food deceptive orchids report a positive correlation between flower/inflorescence size and pollinaria removal and/or fruit set (Schemske 1980; Fritz and Nilsson 1996) whereas in others, flower size has little impact on fruit set (Sabat and Ackerman 1996; Pellegrino et al. 2005) or selection for smaller flowers is found (O'Connell and Johnston 1998). Floral height correlates positively with reproductive success in *Cypripedium acaule* (O'Connell and Johnston 1998). Pollinator-imposed selection may generally vary with abundances of different pollinator species over years, and different trade-offs and constraints may influence evolution of floral traits in the plants (Schemske 1980; O'Connell and Johnston 1998).

Flowers of the sexually deceptive *Chiloglottis trapeziformis* are significantly larger than females of the pollinator species and produce up to 100 times more of the attractive odor compound (Schiestl 2004). The pollinators prefer larger females and larger amount of scent, which may explain the evolution of such exaggerated floral traits (Fig. 2). In *C. trapeziformis* and *C. valida* the pollinators show a preference for dummy females presented at different heights matching the height differences in the respective orchid species (Schiestl and Peakall in press). The pollinator of *C. trilabra* also selects for floral height, but the natural mean height of plants is lower than the experimentally determined optimum for visitation, indicating pollinator-mediated selection cannot explain the precise floral height of this species (Peakall and Handel 1993).

Do orchids impose selection on their pollinators?

There is good evidence that pollinator behavior imposes selection on plants, but do plants also select for pollinator traits? In general, evolutionary change in orchid–pollinator interaction is best viewed as one-sided, i.e. plants responding to pollinator-imposed selection but not vice versa (Dafni 1984; Nilsson 1992; Wasserthal 1997). The evolutionary direction of a mimicry system is, however, determined by the fitness impacts the mimic may have on a model or operator species (Stowe 1988). In the Australian sexually deceptive *Chiloglottis trapeziformis*, pollinators are unable to discriminate between the odor of orchid flowers and the female sex pheromone (Wong and Schiestl 2002), and avoid areas where the unrewarding orchid flowers occur (Peakall 1990). Under certain circumstances, such as when populations of wasps and orchids largely overlap, this could lead to an interruption of the normal mating behavior of the pollinator insects. This will have fitness costs to the model, i.e. if the wingless females of the pollinator species are unable to obtain a mate when calling from within a patch of orchids (Wong and Schiestl 2002). The model may therefore be selected to avoid orchids, and field experiments suggest that females can respond by walking out of an orchid patch, which will resume their attractiveness for males (Wong et al. 2004). Walking a few meters after unsuccessful calling may have evolved specifically in species exploited by orchids, however, experimental tests are lacking.

Evolution of deception in orchids

Despite the strong interest in floral mimicry among evolutionary biologists, its spectacular evolution in orchids still poses a number of unsolved questions. It seems paradoxical that deceptive orchids often show considerably lower fruit set than rewarding species (Neiland and Wilcock 1998; Tremblay et al. 2005), e.g. only 2% in *Cypripedium* during a 10 year survey (Gill 1989), yet deception has evolved in a large number of species, many times independently within the family (Dafni and Bernhardt 1990; Cameron et al. 1999; Cozzolino et al. 2001; Kores et al. 2001; Bateman et al. 2003). Although sexual deception is clearly a derived trait among the orchids (Kores et al. 2001; Bateman et al. 2003), food deception, or at least nectarless flowers, may actually be an ancestral trait in the orchids, suggested by the nectarless flower of primitive orchid groups such as *Apostasia* and *Neuwiedia,* that are pollen-rewarding (Kocyan and Endress

2001). In certain genera such as *Disa* and *Anacamptis,* nectar reward has clearly evolved secondarily from food deception (Johnson et al. 1998; Cozzolino et al. 2001).

A number of hypotheses have been proposed to account for the evolution of deception, i.e. *costs of nectar*, *low density*, *pollinia*, *pollinia loss*, *better isolation*, and *pollinia removal*, described in Bergström (1978), Dressler (1981), Dafni (1987), Nilsson (1992), and Smithson and Gigord (2002), that are little tested or did not gain empirical support. One hypothesis that has been supported by recent empirical investigations is the *outcrossing hypothesis*, proposing that deception reduces geitonogamous pollination (pollen transfer between flowers of an inflorescence) and promotes longer distance pollen flow, because pollinators will visit fewer flowers on an inflorescence, and fly greater distances after being deceived (Dressler 1981). Geitonogamy may reduce female fitness if inbred seeds develop slower or are aborted in early stages of development due to inbreeding depression (Peakall and Beattie 1996; Johnson et al. 2004). Geitonogamy may also impact on male function, since less pollen will be available for export. Many orchids transfer their pollen in pollinia, making fertilization highly efficient, and thus the impacts of geitonogamy more severe. For perennial plants that produce thousands of minute seeds per capsule, like many orchids, the production of fewer, but high-quality fruits, and the maximization of pollen export may increase lifetime reproductive success (Peakall and Beattie 1996). Field studies confirm that pollinators, when visiting deceptive orchids, usually probe a few flowers and then depart quickly (Nilsson 1980; Nilsson 1984; Peakall and Beattie 1996; Ayasse et al. 2000; Johnson 2000). In flowers of *Anacamptis morio* supplemented with nectar, bees probe more and stay longer on flowers, take up more pollinia and cause more self-pollination through geitonogamy (Johnson and Nilsson 1999; Smithson 2002; Johnson et al. 2004). Modeling pollen export in *A. morio* suggest that deceptive flowers export more pollen compared to rewarding ones, when pollinators are abundant and most pollinaria are removed from the flowers (Johnson et al. 2004). In the sexually deceptive *Caladenia tentaculata*, pollinators tend to leave a patch of orchids after pseudocopulation and 87% of pollinations are outcrossing (Peakall and Beattie 1996). Mean distance of pollen flow, detected by tracking stained pollinia, is 15.2 m, which is significantly greater than the mean nearest neighbor distance, and maximum distance of pollen flow is 58 m. In the sexually deceptive *Drakea glyptodon*, pollinators fly an impressive mean distance of 32 m (maximum 132 m) after pseudocopulation at experimentally presented flowers (Peakall 1990). Males of the solitary bee *Colletes cunicularius*, which pollinates four species of *Ophrys*, fly an average distance of 5 m during their patrolling flights, with maximum of 50 m (Peakall and Schiestl 2004). Thus, many studies, especially of sexually deceptive systems, indicate that deception promotes outcrossing, and the low-fruit set in these pollination systems should not be viewed as an indication of a sub-optimal life history (Gill 1989), as it probably is the outcome of a well-balanced trade-off. However, little understood examples are the clonal *Leporella fimbriata*, that is pollinated by pseudocopopulating male ants, and 88% of vector flight are within bounds of clones, and consequently high rates of selfing are expected (Peakall and James 1989). Thus, more data are required to conclusively identify selection driving the evolution of deception.

An alternative view, applying only to the evolution of sexual deception, is its opening of new pollination-niches. Sexually deceptive orchids are unique for their exclusive and effective usage of male insects as pollinators. The key innovation in this system has obviously been the mimicry of mating signals for the attraction of males, enabling the plants to use an array of new pollination niches, i.e. the pool of male insects available as potential pollinators. Adaptation to different pollinator-males required the diversification of mating signals mimicry according to different mate-communication channels. In this scenario, the obtaining of an actual advantage compared to the ancestral pollination system is not a necessary prerequisite.

Evolutionary consequences: patterns of speciation

Food and sexually deceptive orchids show distinct patterns of speciation and mechanisms of reproductive isolation. Food deceptive species are often less specific in pollinator attraction (Cozzolino et al. in press) and thus postzygotic reproductive isolation may be important for the maintenance of species barriers. In sexually deceptive orchids, however, high specificity in pollination accounts for prezygotic isolation (Paulus and Gack 1990; Bower 1996) and post-mating barriers are often lacking (Ehrendorfer 1980). Accordingly, karyotype differences have been found to be larger in food deceptive than in sexually deceptive orchids (Cozzolino et al. 2004).

Sexually deceptive orchids may represent a prime example of sympatric speciation, because high pollinator specificity is linked to differences in the floral odor. Sympatric speciation is predicted when alleles connected to reproductive isolation, e.g. mutations altering floral odor, are strongly selected and therefore become established in the presence of gene flow (Maynard Smith 2002; Rieseberg et al. 2003). Odor differences among orchid species are often small, e.g. in the closely related *Ophrys fusca* and *O. bilunulata*, where a similar set of cuticular hydrocarbons are active in the pollinators, but the relative amounts of the compounds differ significantly from each other (Schiestl and Ayasse 2002). The active floral odor of *O. sphegodes* also differs from *O. exaltata* only by the relative abundances of the active compounds (Mant et al. in press c). These data indicate that among certain *Ophrys* species, a mechanism of pattern recognition of cuticular hydrocarbons in male bees mediates the specificity of pollinator attraction. Changes in the expression of genes responsible for the production of these compounds may thus lead to a change in hydrocarbon pattern and alter pollinator attraction. In *Chiloglottis*, several species differ only in functional groups of one compound that is responsible for pollinator attraction (Mant and Schiestl unpublished). In this system it seems even more obvious that few mutations can change the floral trait mediating reproductive isolation.

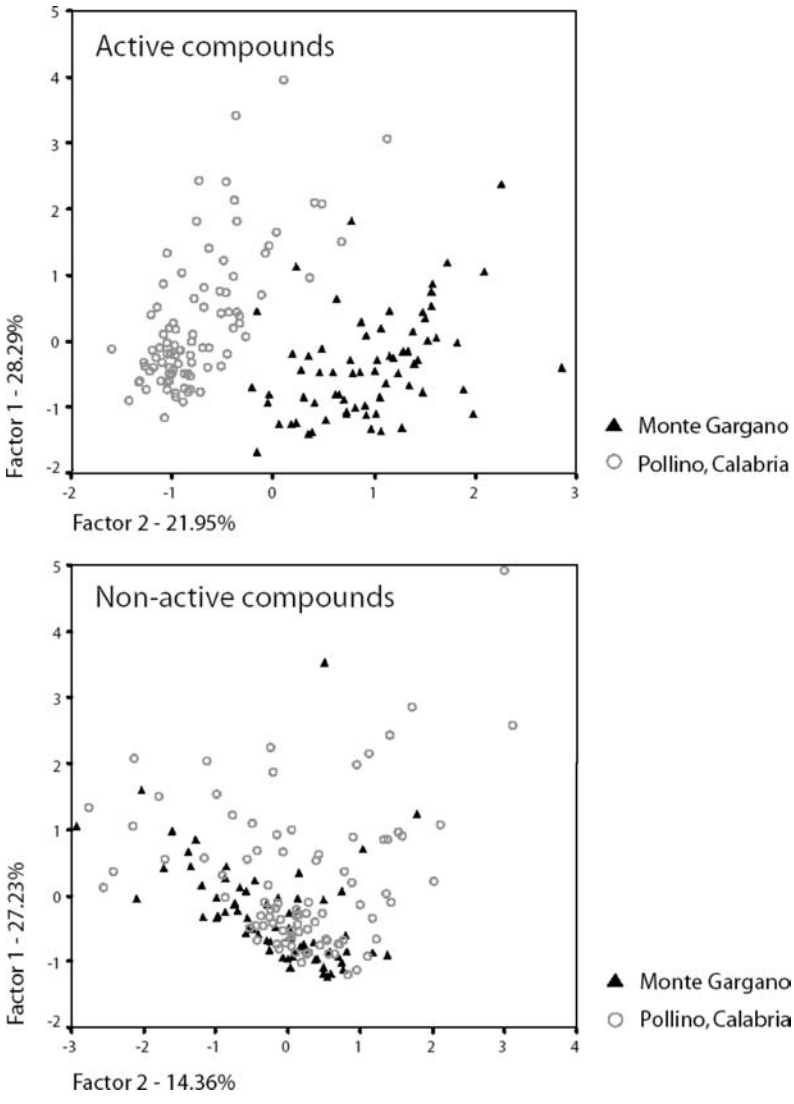

Fig. 4 Population differentiation in floral odor in *Ophrys exaltata* from southern Italy. Two principle components are plotted for active and non-active floral odor compounds in the same individuals of two populations in southern Italy. Active compounds, that attract the pollinator, *Colletes cunicularius* (Mant et al. in press b), are stronger differentiated than non-active compounds indicating diversifying selection on population-specific bouquets, mediated by preferences of the pollinators (Mant et al. in press c)

The lack of post-mating barriers to gene flow, and the predominance of ethological isolation mediated by pollinators has other important consequences for speciation in sexually deceptive orchids. The major independently derived genera, *Ophrys*, *Chiloglottis,* and *Caladenia*, show a characteristic pattern in species differentiation, with little morphological and genetic differences among species within genera or subgeneric clades (Soliva et al. 2001; Jones et al. 2001; Mant et al. 2002; Bateman et al. 2003; Mant et al. in press a). Further, population genetic analyses confirmed a large degree of sharing of microsatellite and AFLP variation among sympatric taxa (Soliva and Widmer 2003; Mant et al. in press a). One interpretation of these patterns is a rapid, recent origin of the taxa and their similarity representing shared ancestral variation. Recent and "explosive" speciation in *Ophrys* has already been assumed by early authors (Kullenberg and Bergström 1976). However, in a global view, a recent origin needs to be assumed for many independent lineages, both within (Mant et al. in press a) and among genera in Europe (*Ophrys*) and Australia (*Chiloglottis*, *Caladenia*). Therefore, it seems more likely that the apparent pattern should be attributed to gene flow among species. Even in the presence of introgression, selection mediated by pollinator preferences for species-specific odor bouquets may nevertheless maintain differences among species (Fig. 4; Mant et al. in press c). Selection may, however, vary among populations, since pollinators can have different degrees of specificity in their responses to sex pheromones (Mant et al. in press c; Vereecken and Schiestl unpublished) or pollinator communities can change with time. Such fluctuations in selective agent may cause orchid species to oscillate between merge and diverge (Grant et al. 2004) and evolve as syngameon (Mant et al. in press a) as suggested for other plants lacking postzygotic reproductive isolation like the genus *Aquilegia* (Hodges and Arnold 1994).

Conclusions

Orchids provide exceptional model organisms for plant-pollinator research with the diversity of such interactions

unmatched by any other group of plants, enabling unlimited possibilities for comparative research. Further, male reproductive success can be monitored quantitatively in orchids through tracking of pollen flow, export, and loss using stained pollinia or microtags (Peakall 1989; Nilsson et al. 1992; Johnson et al. 2004). Generally, we know little about how selection varies through female and male function in hermaphroditic plants.

Our understanding of the ultimate causes of the evolution of deception in orchids remains very incomplete, and we need more studies addressing the link between deception and outbreeding, offspring quality, lifetime reproductive success, and the usage of pollinator niches. Comparative investigations with other plant groups having pollinia, e.g. the Asclepiadaceae (now included in the Apocynaceae) may shed light on the role of pollinia in the evolution of deception. Evolutionary consequences of pollination by deception may include sympatric speciation in sexually deceptive species with high-pollinator specificity. On the other hand, gene flow among species may converge sympatric taxa when pollinator-imposed selection varies. Questions relating to strengths and dynamics of selection imposed by pollinators, variation in floral traits and their heritability, extent of gene flow among sympatric species, and hybrid fitness should be addressed to resolve mechanisms of speciation in these fascinating plants. A new and exciting research direction concerns the genetic bases of floral traits linked to reproductive success and-isolation of plants. Although orchids are, through their long generation times and difficulties in breeding less suitable for QTL studies, extended knowledge about gene functions in model species like *Arabidopsis* and *Oryza* make it now possible to identify target genes in non-model plants like orchids. Knowledge about genes encoding important floral traits in orchids will give insights into molecular evolution of these genes and reveal historical patterns of selection (Rieseberg et al. 2003).

Orchids are extremely rich in species and speciation rates presumed to be exceptionally high (Gill 1989). Although it has often been hypothesized that this spectacular diversification is linked to the intimate and sometimes bizarre interaction of many species with their pollinators (Darwin 1885), we are still facing the challenge of explaining how these mechanisms work and why they have evolved.

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References

Ackerman JD (1981) Pollination biology of *Calypso bulbosa* var. *occidentalis* (Orchidaceae): a food-deception system. Madrono 28(3):101–110

Ackerman JD (1986) Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1:108–113

Ackerman JD, Melendez-Ackerman EJ, Salguero-Faria J (1997) Variation in pollinator abundance and selection of fragrance phenotypes in an epiphytic orchid. Am J Bot 10:1383–1390

Ågren L, Kullenberg B, Sensenbaugh T (1984) Congruences in pilosity between three species of *Ophrys* (Orchidaceae) and their hymenopterean pollinators. Nova Acta Reg Soc Sci Ups Ser V:15–25

Aragon S, Ackerman JD (2004) Does flower color variation matter in deception pollinated *Psychilis monensis* (Orchidaceae). Oecologia 138:405–413

Ayasse M, Schiestl FP, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W (2000) Evolution of reproductive strategies in the sexually deceptive orchid *Ophrys sphegodes*: How does flower-specific variation of odor signals influence reproductive success? Evolution 54(6):1995–2006

Ayasse M, Schiestl FP, Paulus HF, Ibarra F, Francke W (2003) Pollinator attraction in a sexually deceptive orchid by means of unconventional chemicals. Proc R Soc Lond B 270:517–522

Barkman TJ, Beaman JH, Gage DA (1997) Floral fragrance variation in *Cypripedium*: implications for evolutionary and ecological studies. Phytochemistry 44:875–882

Bateman RM, Hollingsworth PM, Preston J, Yi-Bo L, Pridgeon AM, Chase MW (2003) Molecular phylogenetics and evolution of Orchidinae and selected Habenariinae (Orchidaceae). Bot J Linn Soc 142:1–40

Bergström G (1978) Role of volatile chemicals in *Ophrys*-pollinator interactions. In: Harborne G (ed) Biochemical aspects of plant and animal coevolution. Academic Press, New York, pp 207–230

Bergström G, Birgersson G, Groth I, Nilsson AL (1992) Floral fragrance disparity between three taxa of lady's slipper *Cypripedium calceolus* (Orchidaceae). Phytochemistry 31:2315–2319

Blanco MA, Barboza G (2005) Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. Ann Bot 95:763–772

Bogdany FJ (1978) Linking of learning signals in honey bee orientation. Behav Ecol Sociobiol 3:323–336

Borg-Karlson A-K (1990) Chemical and ethological studies of pollination in the genus *Ophrys* (Orchidaceae). Phytochemistry 29(5):1359–1387

Bower CC (1996) Demonstration of pollinator-mediated reproductive isolation in sexually deceptive species of *Chiloglottis* (Orchidaceae: Caladeniinae). Aust J Bot 44:15–33

Cameron KM, Chase MW, Whitten MW, Kores PJ, Jarrell DC, Albert VA, Yukawa T, Hills HG, Goldman DH (1999) A phylogenetic analysis of the Orchidaceae: evidence from RBCL nucleotide sequences. Am J Bot 86(2):208–224

Coleman E (1927) Pollination of the orchid *Cryptostylis leptochila*. Victorian Naturalist 44:20–22

Cozzolino S, Aceto S, Caputo P, Widmer A, Dafni A (2001) Speciation processes in eastern Mediterranean *Orchis* s.l. species: molecular evidence and the role of pollination biology. Isr J Pl Sci 49:91–103

Cozzolino S, D'Emerico S, Widmer A (2004) Evidence for reproductive isolate selection in Mediterranean orchids: karyotype differences compensate for the lack of pollinator specificity. Biol Lett 271:259–262

Cozzolino S, Schiestl FP, Müller A, De Castro O, Nardella A, Widmer A (in press) Evidence for pollinator sharing in Mediterranean nectar mimic orchids: absence of premating barriers? Proc R Soc Lond B

Dafni A, Ivri Y (1981) Floral mimicry between *Orchis israelitica* Baumann and Dafni (Orchidaceae) and *Bellevalia felexuosa* Boiss (Liliaceae). Oecologia 49:229–232

Dafni A (1983) Pollination of *Orchis caspia* – a nectarless plant which deceives the pollinators of nectariferous species from other plant families. J Ecol 71:467–474
Dafni A (1984) Mimicry and deception in pollination. Annu Rev Ecol Syst 15:259–278
Dafni A (1987) Pollination in *Orchis* and related genera: evolution from reward to deception. In: Arditti J (ed) Orchid Biology: reviews and perspectives. Cornell University Press, Ithaca and London, pp 79–104
Dafni A, Bernhardt P (1990) Pollination of terrestrial orchids of southern Australia and the Mediterranean region. In: Hecht MK, Wallace B, Macintyre RJ (eds) Evolutionary Biology 24. Plenum Press, New York, pp 193–252
Darwin C (1885) On the various contrivances by which orchids are fertilised by insects, 2nd edn. John Murray, London
Daumann E (1971) Zum Problem der Täuschblumen. Preslia 43:304–317
Dressler R (1981) The orchids – natural history and classification. Harvard Univ Press, Cambridge, MA
Ehrendorfer F (1980) Hybridisierung, Polyploidie und Evolution bei europäisch-mediterranen Orchideen. Die Orchidee Sonderheft 15–34
Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon Press, Oxford
Fritz A-L, Nilsson A (1996) Reproductive success and gender variation in deceit-pollinated orchids. In: Lloyd DG, Barrett SCH (eds) Floral biology: studies on floral evolution in animal-pollinated plants. Chapman & Hall, New York, pp 319–338
Galizia CG, Kunze J, Gumbert A, Borg-Karlson A-K, Sachse S, Markl C, Menzel R (2005) Relationship of visual and olfactory signal parameters in a food-deceptive flower mimicry system. Behav Ecol 16:159–168
Gigord LDB, Macnair MR, Smithson A (2001) Negative frequency dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soò. Proc Natl Acad Sci 98:6253–6255
Gigord LDB, Macnair MR, Stritesky M, Smithson A (2002) The potential for floral mimicry in rewardless orchids: an experimental study. Proc R Soc Lond B 269:1389–1395
Gill DE (1989) Fruiting failure, pollinator inefficiency, and speciation in orchids. In: Otte D, Endler JA (eds) Speciation and its consequences. Sinauer Associates, Sunderland, pp 458–481
Grant PR, Grant BR, Markert JA, Keller L, Petren K (2004) Convergent evolution of Darwin's Finches caused by introgressive hybridization and selection. Evolution 58(7):1588–1599
Gumbert A, Kunze J (2001) Colour similarity to rewarding model affects pollination in a food deceptive orchid, *Orchis boryi*. Biol J Linn Soc 72:419–433
Heinrich B (1975) Bee flowers: a hypothesis on flower variety and blooming times. Evolution 29:325–334
Hodges SA, Arnold ML (1994) Columbines – a geographically widespread species flock. Proc Natl Acad Sci 91:5129–5132
Johnson SD (1994) Evidence for Batesian mimicry in a butterfly-pollinated orchid. Biol J Linn Soc 53:91–104
Johnson SD, Steiner KE (1997) Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchiaceae). Evolution 51:45–53
Johnson SD, Linder HP, Steiner KE (1998) Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). Am J Bot 85:402–411
Johnson SD, Nilsson LA (1999) Pollen carryover, geitonogamy, and the evolution of deceptive pollination systems in orchids. Ecology 80(8):2607–2619
Johnson SD (2000) Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behavior. Biol J Linn Soc 71:119–132
Johnson SD, Alexandersson R, Linder HP (2003a) Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. Biol J Linn Soc 80:289–304
Johnson SD, Craig PI, Nilsson AL, Ågren J (2003b) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology 84(11):2919–2927
Johnson SD, Craig PI, Ågren J (2004) The effects of nectar addition on pollen removal and geitonogamy in the non-rewarding orchid *Anacamptis morio*. Proc R Soc Lond B 271:803–809
Jones DL, Clements ML, Sharma IK, Mackenzie AM (2001) A new classification of *Caladenia* R. Br. (Orchidaceae). The Orchadian 13:389–419
Kocyan A, Endress PK (2001) Floral structure and development of *Apostasia* and *Neuwiedia* (Apostasioideae) and their relationships to other Orchidacea. Int J Plant Sci 162(4):847–867
Kores PJ, Molvray M, Weston PH, Hopper SD, Brown AP, Cameron KM, Chase MW (2001) A phylogenetic analysis of Diurideae (Orchidaceae) based on plastid DNA sequence data. Am J Bot 88:1903–1914
Kullenberg B (1961) Studies in *Ophrys* pollination. Almquist & Wiksells Boktrykeri AB, Uppsala
Kullenberg B, Bergström G (1976) Hymenoptera aculeata as pollinators of *Ophrys* orchids. Zool Scr 5:13–23
Kunze J, Gumbert A (2001) The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. Behav Ecol 12:447–456
Lammi A, Kuitunen M (1995) Deceptive pollination of *Dactylorhiza incarnata:* an experimental test of the magnet species hypothesis. Oecologia 101:500–503
Laverty TM (1992) Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89:502–508
Mant J, Schiestl FP, Peakall R, Weston PH (2002) A phylogenetic study of pollinator conservatism among sexually deceptive orchids. Evolution 56:888–898
Mant J, Peakall R, Weston P (in press a) Specific pollinator attraction and the diversification of sexually deceptive *Chiloglottis* (Orchidaceae). Pl Syst Evol
Mant J, Brändli C, Vereecken NJ, Schulz CM, Francke W, Schiestl FP (in press b) Cuticular hydrocarbons as sex pheromone of the bee *Colletes cunicularius* and the key to its mimicry by the sexually deceptive orchid, *Ophrys exaltata*. J Chem Ecol
Mant J, Peakall R, Schiestl FP (in press c) Does selection on floral odor promote differentiation among populations and species of the sexually deceptive orchid genus, *Ophrys*? Evolution
Maynard Smith J (2002) Evolutionary genetics. Oxford University Press, Oxford
Menzel R (1985) Learning in honey bees in an ecological and behavioral context. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology. Gustav Fischer, Stuttgart, pp 55–74
Moya S, Ackerman JD (1993) Variation in the floral fragrance of *Epidendrum ciliare* (Orchidaceae). Nord J Bot 13:41–47
Neiland MRM, Wilcock CC (1998) Fruit set, nectar reward, and rarity in the Orchidaceae. Am J Bot 85:1657–1671
Nilsson AL (1979) Anthecological studies of the Lady's Slipper, *Cypripedium calceolus* (Orchidaceae). Bot Notiser 132:329–347
Nilsson AL (1980) The pollination ecology of *Dactylorhiza sambucina* (Orchidaceae). Bot Notiser 133:368–385
Nilsson AL (1983) Mimesis of bellflower (*Campanula*) by the red helleborine orchid *Cephalanthera rubra*. Nature 305:799–800
Nilsson AL (1984) Anthecology of *Orchis morio* (Orchidaceae) at its outpost in the north. Nov Acta Reg Soc Sci Ups V:(C3):167–179
Nilsson AL (1988) The evolution of flowers with deep corolla tubes. Nature 334:147–149
Nilsson AL (1992) Orchid pollination biology. TREE 7(8):255–259
Nilsson LA, Rabakonandriana E, Pettersson B (1992) Exact tracking of pollen transfer and mating in plants. Nature 360:666–668
O'Connell LM, Johnston M (1998) Male and female pollination success in a deceptive orchid, a selection study. Ecology 79(4):1246–1260
Paulus HF, Gack C (1990) Pollinators as prepollinating isolation factors: Evolution and speciation in *Ophrys* (Orchidaceae). Isr J Bot 39:43–79
Peakall R, James SH (1989) Outcrossing in an ant pollinated clonal orchid. Heredity 62:161–167
Peakall R (1989) A new technique for monitoring pollen flow in orchids. Oecologia 79:365–365

Peakall R (1990) Responses of male *Zaspilothynnus trilobatus* Turner wasps to females and the sexually deceptive orchid it pollinates. Funct Ecol 4:159–167

Peakall R, Handel SN (1993) Pollinators discriminate among floral heights of a sexually deceptive orchid: implications for selection. Evolution 47(6):1681–1687

Peakall R, Beattie AJ (1996) Ecological and genetic consequences of pollination by sexual deception in the orchid *Caladenia tentactulata*. Evolution 50(69):2207–2220

Peakall R, Schiestl FP (2004) A mark-recapture study of male *Colletes cunicularius* bees: implications for pollination by sexual deception. Behav Ecol Sociobiol 56:579–584

Pellegrino G, Caimi D, Noce ME, Musacchio A (2005) Effects of local density and flower color polymorphism on pollination and reproduction in the rewardless orchid *Dactylorhiza sambucina* (L.) Soò. Plant Syst Evol 251:119–129

Petterson B, Nilsson AL (1993) Floral variation and deceit pollination in *Polystachya rosea* (Orchidaceae) on an inselberg in Madagascar. Opera Bot 121:237–245

van der Pijl L, Dodson CH (1966) Orchid flowers / Their pollination and evolution. University of Miami Press, Coral Gables

Pridgeon AM, Bateman RM, Cox AV, Hapemann JR, Chase MW (1997) Phylogenetics of subtribe Orchidinae (Orchidoideae, Orchidaceae) based on nuclear ITS sequenes. 1. Intergeneric relationships and polyphyly of *Orchis* sensu lato. Lindleyana 12(2):89–109

Pouyanne A (1917) La fecundation des *Ophrys* par les insectes. Bull Société d'Histoire Naturelle l'Afrique du Nord 8:6–7

Rieseberg LH, Church SA, Morjan CL (2003) Integration of populations and differentiation of species. New Phytologist 161:59–69

Roubik DW (2000) Deceptive orchids with Meliponini as pollinators. Plant Syst Evol 222(1–4):271–279

Roy BA, Widmer A (1999) Floral mimicry: a fscinating yet poorly understood phenomenon. Trop Plant Sci 4(8):325–330

Rudall PJ, Bateman RM, Fay MF, Eastman A (2002) Floral antomy and systematics of Alliaceae with particular reference to *Gilliesia*, a presumed insect mimic with strongly zygomorphic flowers. Am J Bot 89:1867–1883

Sabat AM, Ackerman JD (1996) Fruit set in a deceptive orchid: the effect of flowering phenology, display size, and local floral abundance. Am J Bot 83(9):1181–1186

Schemske DW (1980) Evolution of floral display size in the orchid *Brassavola nodosa*. Evolution 34(3):489–493

Schiestl FP, Ayasse M, Paulus HF, Erdmann D, Francke W (1997) Variation of floral scent emission and post pollination changes in individual flowers of *Ophrys sphegodes* subsp. *sphegodes* (MILLER). J Chem Ecol 23(12):2881–2895

Schiestl FP, Ayasse M, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W (1999) Orchid pollination by sexual swindle. Nature 399:421–422

Schiestl FP, Ayasse M, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W (2000) Sex pheromone mimicry in the Early Spider Orchid (*Ophrys sphegodes*): patterns of hydrocarbons as the key mechanism for pollination by sexual deception. J Comp Physiol A 186:567–574

Schiestl FP, Ayasse M (2002) Do changes in floral odor cause speciation in sexually deceptive orchids? Plant Syst Evol 234(1–4):111–119

Schiestl FP, Marion-Poll F (2002) Detection of physiologically active flower volatiles using gas chromatography coupled with electroantennography. In: Jackson JF, Linskens HF, Inman R (eds) Molecular Methods of Plant Analysis, vol 21, Analysis of Taste and Aroma. Springer, Berlin, pp 173–198

Schiestl FP, Peakall R, Mant J, Ibarra F, Schulz C, Francke S, Francke W (2003) The chemistry of sexual deception in an orchid–wasp pollination system. Science 302:437–438

Schiestl FP, Peakall R, Mant J (2004) Chemical communication in the sexually deceptive orchid genus *Cryptostylis*. Bot J Lin Soc 144:199–205

Schiestl FP (2004) Floral evolution and pollinator mate-choice in a sexually deceptive orchid. J Evol Biol 17:67–75

Schieste FP, Peakall R (in press) Two orchids attract different pollinators with the same floral odor compound: ecological and evolutionary implications

Singer RB (2002) The pollination mechanism in *Trigonidium obtusum* Lindl (Orchidaceae : Maxillariinae): sexual mimicry and trap-flowers. Ann Bot 89:157–163

Singer RB, Flach A, Koehler S, Marsaioli AJ, Amaral ME (2004) Sexual mimicry in *Mormolyca ringens* (Lindl.) Schltr. (Orchidaceae: Maxillariinae). Ann Bot 93:755–762

Smithson A, Macnair MR (1996) Frequency-dependent selection by pollinators: mechanisms and consequences with regard to behaviour of bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). J Evol Biol 9:571–588

Smithson A (2002) The consequences of rewardlessness in orchids: reward-supplementation experiments with *Anacamptis morio* (Orchidaceae). Am J Bot 89:1579–1587

Smithson A, Gigord LDB (2002) Are there fitness advantages in being a rewardless orchid? Reward supplementation experiments with *Barlia robertiana*. Proc R Soc Lond B 268:1435–1441

Soliva M, Kocyan A, Widmer A (2001) Molecular phylogenetics of the sexually deceptive orchid genus *Ophrys* (Orchidaceae) based on nuclear and chloroplast DNA sequences. Mol Phyl Evol 20(1):78–88

Soliva M, Widmer A (2003) Gene flow across species boundaries in sympatric, sexually deceptive *Ophrys* (Orchidaceae) species. Evolution 57:2252–2261

Sprengel CK (1793) Das entdeckte Geheimniss in der Natur im Bau und in der Befruchtung der Blumen. Translation in Lloyd DG, Barrett SCH (eds) Floral Biology. Chapman & Hall, New York, pp 3–43

Steiner KE, Whitehead VB, Johnson SD (1994) Floral pollinator divergence in two sexually deceptive South African orchids. Am J Bot 81(2):185–194

Steiner KE (1998) The evolution of beetle pollination in a South African orchid. Am J Bot 85:1180–1193

Stowe MK (1988) Chemical mimicry. In: Spencer KC (ed) Chemical mediation of coevolution. Academic Press, San Diego, pp 513–587

Thakar JD, Krushnamegh K, Chauhan AK, Watve AV, Watve MG (2003) Nectarless flowers: ecological correlates and evolutionary stability. Oecologia 136:565–570

Thompson JD (1978) Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. Am Midland Naturalist 100:431–440

Tremblay RL (1992) Trends in the pollination ecology of the orchidaceae: evolution and systematics. Can J Bot 70:642–650

Tremblay RL, Ackerman JD, Zimmerman JK, Calvo RN (2005) Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. Biol J Linn Soc 84:1–54

Vogel S (1983) Ecophysiology of zoophilic pollination. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of Plant Physiology, Physiological plant ecology, new series, vol. 12c. Springer, Berlin, pp 560–611

Vogel S (1993) Betrug bei Planzen: Die Täuschblumen. 1. Akademie der Wissenschaften und der Literatur, Mainz, Franz Steiner, Stuttgart

Wasserthal LT (1997) The pollinators of the Malagasy Star Orchids *Angraecum sesquipedale, A. sororium* and *A. compactum* and the evolution of extremely long spurs by pollinator shift. Bot Acta 110:343–359

Wiens E (1978) Mimicry in plants. Evol Biol 11:365–403

Wickler W (1968) Mimicry in plants and animals. Weidenfeld and Nicolson, London

Wong BBM, Schiestl FP (2002) How an orchid harms its pollinator. Proc R Soc Lond B 269:1529–1532

Wong BBM, Salzmann C, Schiestl FP (2004) Pollinator attractiveness increases with distance from flowering orchids. Biol Lett 271:212–214

Yadav SR (1995) Pollination biology of the south west asian orchid *Cottonia peduncularis*. Hornbill 1:28–31